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Evidence for specific independence of the shrew (Mammalia: Soricidae) of St. Paul Island (Pribilof Islands, Bering Sea)

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Abstract

The authors define the karyotype (2n 55, NFa 62) of the shrew (subgenus *Otisorex*) inhabiting St. Paul Island (Pribilof Islands), Bering Sea, and present data concerning relationships of that taxon. The somatic chromosomal complement (male) comprised 26 pairs of homologous autosomes, the sex chromosomes X and Y, and one additional chromosome, the smallest of the complement, for which no homologue was identified. The function of this unpaired element is uncertain; that it may be involved in the sex-chromosome system is suggested (a Y_2 has not been recorded in any shrew of the subgenus *Otisorex*). The applicable name for the shrew of St. Paul Island has been questionable for many years and thought to be *Sorex hydrodromus* Dobson, 1889, the problem in part due to imprecise data regarding the type specimen of *S. hydrodromus*. Although type locality for *S. hydrodromus* was given as Unalaska Island (Aleutian Islands, Bering Sea), where no shrew is known to exist, there is evidence that the original specimens were collected somewhere within the rather vast region that formed the governmental unit called Unalaska District by the administrators of Russian America (prior to 1867). The District included the western end of the Alaska Peninsula, the eastern Aleutian Islands, and the Pribilof Islands. That *S. hydrodromus* in dentition is compatible with shrews of the *S. araneus* group (subgenus *Sorex*) has been indicated in the literature. We conclude that the applicable name for the shrew of St. Paul Island is *Sorex* (*Otisorex*) *pribilofensis* Merriam, 1895. The karyotype of *S. pribilofensis* and other taxonomic characters distinguish that species from the three Eurasian members of subgenus *Otisorex*, as well as from all nearctic species for which pertinent data exist. With the exception of that shrew and one species of rodent, the indigenous terrestrial mammals occurring on islands in the Bering Sea differ only subspecifically from those on the two continents. The authors suggest that the precursor of *S. pribilofensis* became established in Beringia during pre-Würm time.

Introduction

The Recent mammalian faunas of the islands in the Bering Sea, within the limits of the former Beringia, consist of species that evidently had occupied highlands that became isolated by rising sea-levels at intervals during Pleistocene time and were able to persist under consequent ecological and spatial constraints. Of the six major islands in the Bering Sea, the four most remote, St. Paul, St. George, St. Matthew, and Hall, have only single species of indigenous mammals (not including the arctic fox, which migrates to and from the islands on the sea-ice, and the polar bear, which formerly was present on some islands during summer). Individuals of other species are carried rarely on drifting ice to St. Lawrence Island. The red fox occurs on Nunivak Island (separated from the Yukon-Kuskokwim river delta on the Alaskan mainland by 30 km-wide Etolin Strait), and probably also freely moves over sea-ice. Three families of small mammals (indigenous) are represented on the Bering Sea Islands: Soricidae, Sciuridae, and Arvicolidae. Four species are holarctic, two are Beringian endemics, and one is nearctic (cf. Rausch and Rausch 1995). In addition, one species, the shrew occurring on St. Paul Island, Pribilof Islands (57°10′ N, 170°15′ W) has been of uncertain identity.

Shrews are present on three of the Beringian islands. *Sorex cinereus hollisteri* Jackson occurs on Nunivak Island, as well as in continental Alaska; the insular population is distinguished by a pale to nearly white pelage. *Sorex cinereus jacksoni* Hall et Gilmore is limited to St. Lawrence Island. The shrew on St. Paul Island has been designated either *Sorex hydrodromus* Dobson or *Sorex pribilofensis* Merriam; herein, we follow the nomenclature applied by van Zyll de Jong (1982, 1991), designating the species as *S. pribilofensis. Sorex cinereus* Kerr and the shrew of St. Paul Island are referable to the subgenus *Otisorex*. In the present report, we describe the karyotype and discuss macromorphologic characteristics of *S. pribilofensis* as well as its status with respect to other amphiberingian species.

Material and methods

During August 1995, we collected three shrews on St. Paul Island (one subadult male, one subadult female, one adult female). Skins and complete skeletons were prepared, and reproductive organs were preserved in 10 per cent formalin solution. Those organs and dental and cranial features were studied by means of a stereoscopic microscope with ocular micrometer graduated in tenths of millimeters. (Skulls from 14 animals and reproductive organs from 2, collected in other years, were useful for comparison.) For definition of the karyotype, cells from marrow and lymphatic tissue were treated with colchicine and hypotonic solution, centrifuged, fixed, and placed on slides; they later were stained in the laboratory at the University of Washington, applying the method of Seabright (1972) for G-banding and that of Sumner (1972) for C-banding. Cells from testes were fixed and stained in acetic orcein. Chromosomes were counted and evaluated in intact cells in metaphase. The karyograms were prepared on the basis of photographs of 10 cells from the male shrew, and by comparison of chromosomes in cells of the three animals.

Measurements of chromosomes were obtained according to the method of Levan et al. (1964). For the karyograms, arm-ratio and size were the bases for assembling pairs of non-banded chromosomes; those with G-bands were identified from banding-pattern and size, and C-banded chromosomes were distinguished by size and by location of centromeric heterochromatin. The sex-chromosomes were determined by differential characteristics. The fundamental number (FN) of chromosomal arms was established following the method of Matthey (1945).

Voucher-specimens have been deposited as follows: Burke Memorial Washington State Museum, University of Washington, No. 39 491; and Museum of Southwestern Biology, University of New Mexico, Nos. 83 326 and 83 327.

Morphometric data for shrews of the *Sorex cinereus* group are not included herein; extensive analyses have been published by van Zyll de Jong (1982, 1991).

Results

The chromosomal preparations from the male shrew included many intact cells in metaphase, in each of which 2 n was 55: 52 autosomes, plus the sex-chromosomes (X and Y), and an additional chromosome for which no homologue was identified. Based on arm-ratio in metaphase, 8 large and 2 very small autosomes were classified as metacentric to submetacentric (range of arm-ratio 1.04 to 2.90); those of the remaining autosomal complement were classified as subtelocentric to acrocentric (range of arm-ratio 2.95 to 10.00) (four of that group, with lower arm-ratios, were perhaps marginally submetacentrics). The X-chromosome was relatively large and submetacentric (arm-ratio 1.88 to 2.75); the Y-chromosome, of intermediate size, was subtelocentric (arm-ratio 2.95 to 4.50). The un-

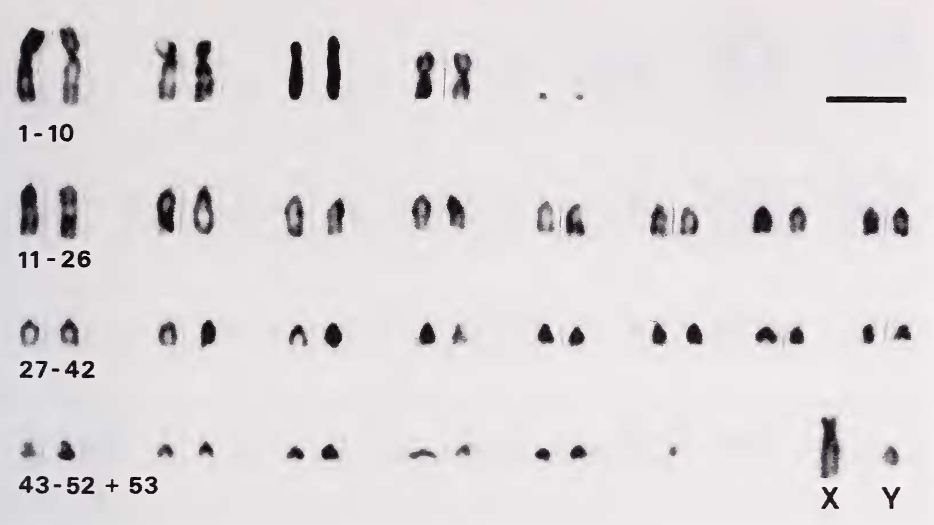

Fig. 1. Karyogram of *Sorex pribilofensis*, male. Standard Giemsa stain. Scale-bar represents 5 micrometers.

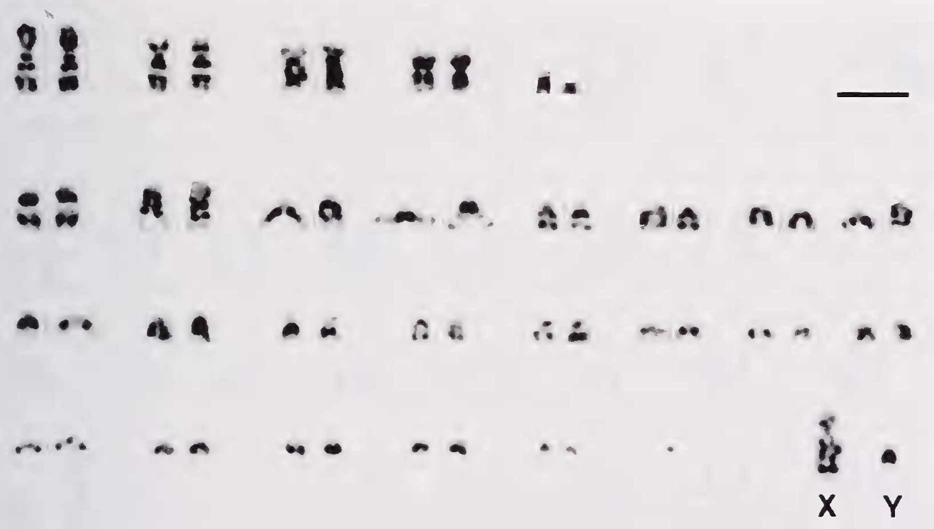

Fig. 2. Karyogram of *S. pribilofensis*, male, G-banded. Arrangement of chromosomes as in Fig. 1. Scale-bar represents 5 micrometers.

paired chromosome was very small and could not be measured with accuracy, although with the microscope at maximal magnification, short arms were discernible, indicating subtelocentric form. In the karyograms (Figs. 1–4), the complements of four cells, with staining as indicated to show characteristics of the individual elements, are arranged by size and conformation: meta/submetacentric autosomes, Nos. 1–10; subtelo/acrocentric autosomes, 11–52; the unpaired chromosome (No. 53) has been placed last, with the autosomes. The X-chromosome evidently was negative for heterochromatin, as were the short

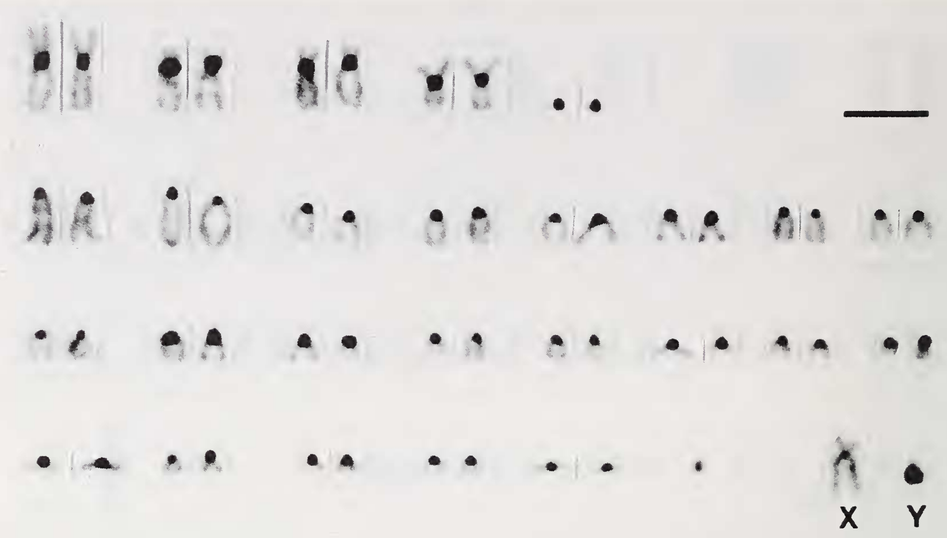

Fig. 3. Karyogram of *S. pribilofensis*, male, C-banded. Arrangement of chromosomes as in Fig. 1. Scale-bar represents 5 micrometers.

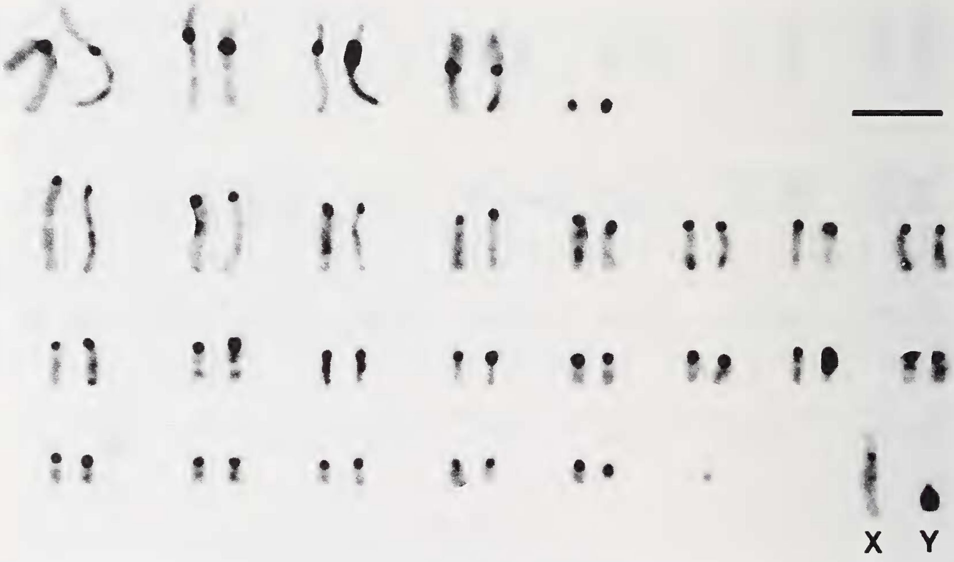

Fig. 4. Karyogram, *S. pribilofensis*, male, C-banding of chromosomes in early metaphase. Arrangement of chromosomes as in Fig. 1. Scale-bar represents 5 micrometers.

arms of the Y-chromosome, and the entire unpaired element. The FN (autosomes, not including chromosome No. 53) was 62. The cultured cells from the two female shrews did not provide preparations of adequate quality and only selected chromosomes could be compared with those of the male; the female diploid number was not certainly determined. In the testicular cells, we found neither mitotic nor meiotic divisions. The significance of chromosome No. 53 was not established.

The adult female was not lactating but had earlier produced young; the uterine cornua, with 5 placental scars on right and 4 on left, were about 2 mm in diameter and each was 8–9 mm in length; length of the vagina was approximately 3.5 mm. The glans penis (adult male) was 1.2 mm in length and 1.5–1.6 mm in width. In lateral view, the anterior surface was truncate, sloping ventrad; the orifice of the urogenital duct on that surface was not discerned. A corona was lacking.

Dentition of all specimens examined corresponded closely with the descriptions and figures of Merriam (1895) and Jackson (1928) for *S. pribilofensis.* The medial tines of the incisors in our material were prominent (about 0.25 mm long when unworn); in form and position, they were much like those of *S. cinereus.*

Discussion

The subgenus *Otisorex* is represented in Eurasia by only three species (Pavlinov and Rossolimo 1987): *Sorex leucogaster* Kuroda, 1933 (syn. *S. beringianus* Yudin, 1967) (type locality: Paramushir Island, Kuril Islands); *S. portenkoi* Stroganov, 1956 (type locality: vicinity of Anadyr', Chukotka); and *S. camtschaticus* Yudin, 1972 (type locality: Kambal' Bay, Kamchatka). The taxonomic status of those species has been discussed in detail (Rausch and Rausch 1995). *Sorex pribilofensis* (2 n 55, FNa 62) is distinct karyotypically from two of the three species of the subgenus *Otisorex* that occur in Eurasia. The karyotype of *S. leucogaster* (2 n 66, FN 70) resembles that of *S. cinereus*; the diploid number of *S. portenkoi* is 60, FN 60 (Ivanitskaia and Kozlovskii 1985). The karyotype of *S. camtschaticus* has not been defined. That taxon was described originally as a subspecies of *S. cinereus* and is distinguished by large size, long tail, and cranial characteristics (Yudin 1972). Well developed fringes of bristle-like hairs laterally bordering the hind feet are present (Yudin 1973). Neither the glans penis nor dentition of *S. camtschaticus* was described by Yudin as notably different; presumably, they closely resemble those of *S. cinereus.* The morphometric analyses of van Zyll de Jong (1982, 1991) support the conclusion that *S. camtschaticus* is an independent species.

The karyotype of *S. pribilofensis* is unlike any known for the subgenus *Otisorex*. In other taxonomic characters as well, the St. Paul Island shrew differs from members of the subgenus occurring at the present time in Alaska (Rausch and Rausch 1995). Only two of those, *S. cinereus* and *S. monticolus* Merriam, are known to have extensive geographic ranges in northwestern North America. *S. c. cinereus* Kerr and *S. c. hollisteri* occur widely in Alaska. *S. monticolus* is represented on the Alaskan mainland by three subspecies; one, *S. m. shumaginensis* Merriam, also inhabits the Shumagin Islands, which are not in Bering Sea but lie near the southern shore of the lower Alaska Peninsula. The patterns of their distribution suggest that the other members of the subgenus *Otisorex* occurring in Alaska dispersed into northwestern North America during post-glacial time; well defined taxonomic characters distinguish each of them from *S. pribilofensis.* (Other nearctic species of subgenus *Otisorex*, evidently also distributed to the south of the continental glacier during Würm/Wisconsin time, are not considered here.)

We were not able to discern karyotypic relationships of *S. pribilofensis* on the basis of Robertsonian chromosomal rearrangements nor of interspecific chromosomal homologies. As in *S. cinereus* (2 n 66, FNa 70), two small submetacentric autosomes were present, and centromeric heterochromatin was present in all autosomes. In the two species, the sex-chromosomes (X and Y) appeared to be similar. In *S. pribilofensis*, the "unpaired" chromosome (No. 53) may be also a sex-chromosome, perhaps Y_2. If so, for the subgenus *Otisorex*, it would be unique.

The uterus of some shrews of the subgenus *Sorex* has been described by Dolgov and Luk'ianova (1966), but little is known of the form of the organ in members of the subgenus *Otisorex*. In the adult female *S. pribilofensis*, the uterus resembled that of *S. cinereus* as illustrated by Yudin (1972) and as we observed in three specimens. The glans penis of *S. pribilofensis* also somewhat resembled that of *S. cinereus.* The glans of "*S. hydrodromus*" was described by Yudin (1969) from a shrew labeled as from "Unalaska Island"; he reported that the organ was 2 mm in length and only 0.7 mm in diameter at the base; the urogenital orifice was within an anterior concavity, enclosed by a peripheral ridge. His illustration (Yudin 1969) indicated that the organ resembled that of *S. pribilofensis.* Yudin (1969) studied the type specimen of *S. hydrodromus* (No. 2389, a female) in the Museum at Leningrad; he did not provide the number of the male specimen he examined.

The applicable name for the species of shrew occurring on St. Paul Island, and its systematic status, have remained uncertain due in part to problems relative to accession numbers of museum-specimens, type locality, and discrepancies in reported descriptions of the dentition and other anatomical characters. A taxon believed to have represented that species was described as *Sorex hydrodromus* by Dobson (1889) on the basis of a specimen in the Zoological Museum of the Russian Imperial Academy of Sciences, St. Petersburg, for which type locality was given as Unalaska Island (Aleutian Islands). The Museum's accession number was not listed by Dobson (1889) but was stated to have been No. 85 by Jackson (1928). Dobson (1889) remarked that the teeth closely resembled those of *Sorex vulgaris* (= *S. vulgaris* Nathusius, 1838 = *S. araneus* L.), and he considered also that the shrew was aquatic, having pedal fringes even more developed than those of *Crossopus fodiens* [= *Neomys fodiens* (Pennant)]. Evidently, the specimen studied by him cannot now be certainly recognized in the collections of the Zoological Museum. On the basis of Dobson's (1889) description and figure of the rostrum and teeth of *S. hydrodromus*, Jackson (1928) listed it as an independent species, but indicated its close similarity to *S. tundrensis* Merriam (*arcticus* group). Jackson (1928) provided a detailed description of *S. pribilofensis*, which he placed in a distinctive group.

At the Zoological Museum also, Hall (in Murie 1959) found the assumed type of *S. hydrodromus* to be an immature female, No. 2389 (Zoological Museum of the Academy of Sciences, Leningrad, U.S.S.R.), collected by I. G. Voznesenskii at "Unalaska", during the period 1840–1848. That specimen and a second *S. hydrodromus* from "Unalaska" (No. 2370) he noted were distinct from specimens of *S. pribilofensis* (Nos. 2437 and 2485, one labeled as collected by Voznesenskii on St. Paul Island) (Hall, in Murie 1959), and he concluded that *S. hydrodromus* was a member of the *S. arcticus* group of shrews. Hoffmann and Peterson (1967) considered that specimens of *S. hydrodromus* were virtually indistinguishable from *S. pribilofensis*, and proposed, in view of the problems concerning types and localities, that the designation *hydrodromus* be suppressed in favor of *pribilofensis* for the species from St. Paul Island.

Those decisions notwithstanding, the uncertainty about the status of *S. hydrodromus* and *S. pribilofensis* has persisted and published opinions concerning it have become increasingly divergent, as shown by the following (a complete review of the numerous Russian literature is not given here). Hall and Kelson (1959) recognized *S. pribilofensis* and listed *S. hydrodromus*, in agreement with Jackson (1928) that it might prove to be identical with "*Sorex arcticus tundrensis*". Yudin (1969) did not favor synonymy for *pribilofensis* until additional taxonomic characters could be compared. Gureev (1979) listed *S. pribilofensis* as an independent species and suggested that *S. hydrodromus* be placed in synonymy with *S. cinereus.* Corbet and Hill (1980) accepted *S. pribilofensis* and did not list *S. hydrodromus.* Junge and Hoffmann (1981) applied the name *S. hydrodromus* to the shrew of St. Paul Island. Hall (1981) listed *S. pribilofensis* as a synonym of *S. hydrodromus*, as did Honacki et al. (1982). Van Zyll de Jong (1982, 1991) designated the shrew on St. Paul Island as *S. pribilofensis*, in the subgenus *Otisorex*. Hutterer (1993) stated that *hydrodromus* is the applicable name for that taxon, on grounds of priority.

S. pribilofensis was applied by Rausch and Rausch (1995). In a major work on insectivores of Siberia (Yudin 1989), it was concluded that *S. hydrodromus* and *S. cinereus camtschatica* (= *S. camtschaticus*) are very similar and that the morphological differences between them are compatible with the wide range of variation exhibited by *S. cinereus*. (That volume, published by his colleagues three years after the untimely death of B. S. Yudin, unfortunately omitted some of the recent Russian literature concerning shrews of subgenus *Otisorex*.)

A major question relating to the status of the taxon designated *S. hydrodromus* is the identification of its type locality, which was recorded as "Unalaska" on specimen-tags by the collector, I. G. Voznesenskii, circa 1840 (Hall, in Murie 1959). The locality "Unalaska" has been judged to mean Unalaska Island, but numerous attempts to find shrews there have been unsuccessful, and the Aleut residents have never recognized that any shrew occurs on the island (see Peterson 1967). Small mammals of two species, a vole, *Microtus oeconomus* (Pallas), and a varying lemming, *Dicrostonyx unalascensis* Merriam, are resident there, however, and at intervals each attains high numerical density. In a written communication, A. A. Gureev stated (in Peterson 1967) that a memorandum in the Russian archives, dated 1842, mentioned two mammals collected on Unalaska Island that were thought to correspond to the two shrews labeled as from "Unalaska". If Voznesenskii (see Hall, in Murie 1959) had opportunity to collect only two mammalian specimens on the Island, it is conceivable that they may have represented one or both species of the arvicolids. Peterson (1967) noted that the designation "Unalaska", as applied by the collector, could have referred to the Russian American "Unalaska District", which encompassed the entire region from the Shumagin Islands at the western end of the Alaska Peninsula, westward to the Fox Islands, and the Pribilof Islands (see Golovin 1862; Dall 1870). The Alaska Peninsula and Unimak Island, the Aleutian Island closest to the mainland, have a continental mammalian fauna, and shrews of at least three species (*S. cinereus*, *S. monticolus*, and *S. tundrensis*) could have been collected within the Unalaska District, in addition to that on St. Paul Island (in the same district). Hall (in Murie 1959) gave data for four shrews: No. 2389, type of *S. hydrodromus*, Unalaska: No. 2370, *Sorex*, Unalaska, also identified as *S. hydrodromus*; No. 2437, *Sorex pribilofensis*, St. Paul Island; and No. 2485. Hall (in Murie 1959) stated that Nos. 2485 and 2437 originated on St. Paul Island; evidently both had been so labeled by the collector. Hall's descriptions (in Murie 1959) indicate that the pigmentation on the cingula of the unicuspids of specimens identified as *hydrodromus* was not compatible with its allocation to the subgenus *Otisorex*, as compared with the specimens from St. Paul Island.

In *S. pribilofensis*, we found the five unicuspids to be graded in size, from the largest (anteriormost) to the smallest (posteriormost), and the first unicuspid slightly longer than the posterior cusp of the incisor; the opposite was shown in *S. hydrodromus* (Dobson 1889). Yudin (1969) also studied specimen No. 2389, and reported that the posterior cusp of the incisor, as in *pribilofensis*, was shorter than the first unicuspid, but the unicuspids were not similarly graded. In the posthumous volume of Yudin (1989), the relative lengths of unicuspids of *S. hydrodromus* (specimen-number not given) did not correspond with his earlier (Yudin 1969) description but exhibited a gradation in length similar to that of *S. pribilofensis* as seen in our material.

Van Zyll de Jong (1982) did not place *S. pribilofensis* in synonymy with *S. hydrodromus*, in view of the substantial doubt existing with regard to the identity of the type of *S. hydrodromus*. He further considered that his comparisons of tail-lengths alone indicated that *S. hydrodromus* and *S. pribilofensis* could not be derived from the same soricid population. His data made clear that the tail-length of *S. hydrodromus* was more than six standard deviations from the mean for *S. pribilofensis*. In agreement with van Zyll de Jong (1982), we retain the designation *Sorex pribilofensis* for the shrew on St. Paul Island. For the specimens of *S. hydrodromus* in St. Petersburg, stated to have been preserved in alcohol, DNA analysis may be a possibility. We attribute significance to the judgements of JACKSON (1928) and HALL (in MURIE 1959) that the specimens designated *S. hydrodromus* represent a member of the *Sorex araneus* group.

The Pribilof Islands lie in the Bering Sea quite near the southern edge of the continental shelf. During the maxima of the last (Würm/Wisconsin) and penultimate (Riss/Illinoian) glacial periods, the present islands existed as highlands on the exposed continental shelf. Sea-level fell probably about 135 m in the Bering Sea during the maximal phase of the penultimate glaciation (HOPKINS 1973). Evidence of glaciation of pre-Würm age exists on St. George Island but not on St. Paul Island (HOPKINS and EINARSSON 1966). Terrestrial mammals inhabiting islands in the Bering Sea with two exceptions represent species of extensive geographic ranges in Beringia during the last glaciation; they differ only subspecifically from Recent species. Two species, *Sorex pribilofensis* and a varying lemming, *Dicrostonyx exsul* Hall et Gilmore on St. Lawrence Island, evidently are of pre-Würm origin, derived from precursors present in Beringia by Riss time. The existence of the brown lemming, *Lemmus sibiricus* KERR, on St. George Island, about 48 km to the north of St. Paul, indicates that the now-submerged areas surrounding the islands were lowlands that supported wet tundra during the Würm period, by which time *S. pribilofensis* probably inhabited the St. Paul highland. The precursor of *S. pribilofensis* was perhaps synchronously present in Beringia with the precursor(s) of the three Recent species of shrews of subgenus *Otisorex* in northeastern Eurasia (*Sorex leucogaster*, *S. portenkoi*, and *S. camtschaticus*). YUDIN (1989) suggested that *S. camtschaticus* may represent a shrew that made its way to Eurasia via the Aleutian Islands, Komandorskie Islands, and Kamchatka. Since no indigenous terrestrial mammals are now present in the Aleutian Islands west of Umnak Island, and since the islands were ice-covered during glacial periods (HOPKINS 1972), that the northern vole and the varying lemming occurring on Unalaska Island and Umnak Island spread westward from the Alaska Peninsula during early postglacial time seems a tenable consideration. Much evidence indicates that the shrew designated *S. hydrodromus* was collected somewhere within the Unalaska District other than on St. Paul or Unalaska Islands. The data support the conclusion that *S. pribilofensis* is specifically distinct from the shrew that was described as *S. hydrodromus.*

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Zusammenfassung

Hinweise auf die artliche Selbständigkeit der Spitzmaus (Mammalia: Soricidae) von der Insel St. Paul (Pribilof Inseln, Beringmeer)

Die Chromosomen von einer auf der Insel St. Paul (Pribilof Inseln) vorkommenden Spitzmausart wurden untersucht. Bei einem männlichen Tier bestand der Karyotyp (2 n = 55) aus 52 Autosomen, den

Geschlechtschromosomen (X und Y), und einem sehr kleinen Chromosom ohne Homologon. Die NFa, ausschließlich dem kleinsten Chromosom, war 62. Zwei Namen, *Sorex hydrodromus* Dobson, 1889 und *S.* (*Otisorex*) *pribilofensis* Merriam, 1895, sind in der Vergangenheit auf diese Spitzmaus verwendet worden. Wie in dieser Arbeit besprochen, weisen die Zähne deutliche Unterschiede auf, die eine artliche Trennung der zwei Taxa begründen. Für die auf der Insel St. Paul vorkommende Spitzmaus verwenden wir den Namen *S. pribilofensis*; die richtige spezifische Bezeichnung für *S. hydrodromus* ist unbekannt. Der Karyotyp bzw. andere Artmerkmale unterscheiden *S. pribilofensis* von den drei Vertretern der Untergattung *Otisorex* in Eurasien, gleichfalls von den nearktischen Arten dieser Untergattung. Die meisten Säugetiere, die Inseln im Beringmeer bewohnen, sind Vertreter (Unterarten) von Säugetieren, die auf dem Festland (Eurasien und Nord-Amerika) weit verbreitet sind. *S. pribilofensis* und ein Halsbandlemming (*Dicrostonyx*) sind aber selbständige Arten, die anscheinend vor der letzten pleistozänen Kaltzeit (Würm) die heutigen Inseln schon besiedelt hatten.

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